

Predation on invasive cane toads (*Rhinella marina*) by native Australian rodents

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Abstract The success of an invasive species can be reduced by biotic resistance from the native fauna. For example, an invader that is eaten by native predators is less likely to thrive than one that is invulnerable. The ability of invasive cane toads (*Rhinella marina*) to spread through Australia has been attributed to the toad's potent defensive chemicals that can be fatal if ingested by native snakes, lizards, marsupials and crocodiles. However, several taxa of native insects and birds are resistant to cane toad toxins. If native rodents are also capable of eating toads (as suggested by anecdotal reports), these large, abundant and voracious predators might reduce toad numbers. Our field observations and laboratory trials confirm that native rodents (*Melomys burtoni*, *Rattus colletti* and *Rattus tunneyi*)

readily kill and consume cane toads (especially small toads), and are not overtly affected by toad toxins. Captive rodents did not decrease their consumption of toads over successive trials, and ate toads even when alternative food types were available. In combination with anecdotal reports, our data suggest that rodents (both native and invasive) are predators of cane toads in Australia. Despite concerns about the decline of rodents following the invasion of toads, our data suggest that the species we studied are not threatened by toads as toxic prey, and no specific conservation actions are required to ensure their persistence.

Keywords Alien species · Biotic resistance · *Bufo marinus* · *Rhinella marina* · Predation · Toxin resistance

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Introduction

Interactions between invasive taxa and native species can affect not only the impact of an invader but also its success or failure in the novel environment. For example, an invader that is readily killed and consumed by native predators is less likely to thrive than one that is invulnerable. Surveys suggest that only a small proportion of translocated taxa thrive in their new environment (Jeschke and Strayer 2006), and one plausible reason for this is biotic resistance (sensu Elton 1958) from native taxa.

Testing this idea in translocated species that fail to establish populations in their new range is difficult; however, even successful invaders that spread widely can be challenged by biotic resistance, which could limit the invader's abundance, distribution and hence its impact (e.g. Dumont et al. 2011).

Although biotic resistance faced by successful invasive species is potentially an important issue, little is known on

this topic. Cane toads (*Rhinella marina*) offer an excellent model system with which to explore this question. Toads have thrived since being introduced to Australia in 1935 (Lever 2001), but simple mathematical models suggest that toads in Australia experience around 99 % mortality between the egg and adult stages (Alford et al. 2006). Causes of mortality remain largely unknown. Abiotic and biotic factors (e.g. breeding ponds drying out, predation by aquatic insects and competition with other tadpoles) can cause mortality for eggs and tadpoles (Alford et al. 1995; Cabrera-Guzmán et al. 2012, 2013). Such effects vary through space and time, but in some instances may be highly significant (e.g. <1 % survival of eggs and hatchlings in the presence of cannibalistic conspecific tadpoles: Alford et al. 1995). In addition, parasitism, cannibalism and predation by ants can reduce survival of metamorph toads (Pizzatto and Shine 2008; Kelehear et al. 2009; Ward-Fear et al. 2010). Predation by vertebrates on this invasive species remains poorly studied (but see, for example, Hamley and Georges 1985; Letnic et al. 2008; Ujvari and Madsen 2009). Conventional wisdom has been that predation by native vertebrate species is unimportant, because the toads have potent chemical defences that are fatal if ingested by native predators (e.g. Covacevich and Archer 1975; Burnett 1997).

Australia lacks native toads, so many lineages of endemic Australian predators have no evolutionary history of exposure to bufonid toxins (Shine 2010). Arrival of toads has caused massive (>90 %) population crashes in predators such as blue-tongued skinks, yellow-spotted monitors, northern quolls and freshwater crocodiles (Doody et al. 2006; Letnic et al. 2008; Ujvari and Madsen 2009; Price-Rees et al. 2010; Woinarski et al. 2010). In vulnerable vertebrates, toad toxins inhibit the Na⁺ K⁺-ATPase enzyme (and thus, disrupt sodium transport across cell membranes), increase myocardial contractility, and cause vasoconstriction and arrhythmia (Flier et al. 1980; Daly et al. 1987; Bagrov et al. 1993). However, there is variation in physiological resistance to bufonid toxins due to interspecific differences in the Na⁺ K⁺-ATPase isozyme (Ujvari et al. 2013). For example, many predatory invertebrates are immune to bufadienolides (the cardioactive steroids in the toad's poison) likely due to important differences in structure and physiology between the cardiac systems of invertebrates and those of vertebrates (Schmidt-Rhaesa 2007). Ants, crayfish, dragonfly nymphs, water beetles and water bugs all consume various toad life history stages without ill effect (Crossland and Alford 1998; Ward-Fear et al. 2010; Cabrera-Guzmán et al. 2012). Some vertebrate species exhibit high tolerance to toad toxins, presumably because they have inherited toad-resistance from ancestral Asian taxa exposed to the bufadienolides of Asian bufonids (Llewelyn et al. 2011). Examples include colubrid snakes

(Phillips et al. 2003) and birds (Beckmann and Shine 2009). However, these predators rarely consume toads if alternative prey are available. Llewelyn et al. (2011) found that keel-back snakes (*Tropidonophis mairii*) took native frogs in preference to toads; and Beckmann and Shine (2011) showed that raptors (black kites *Milvus migrans* and whistling kites *Haliastur sphenurus*) took the road-killed carcasses of frogs in preference to toads. Despite some anecdotal reports of predation on toads by birds, reviews of this topic have concluded that snakes and birds are unlikely to be significant predators of cane toads in Australia (Beckmann and Shine 2009; Shine 2010; Llewelyn et al. 2011). Potentially, rodents (both native and introduced) could be more important predators of invasive toads. Rodents have a higher tolerance to bufotoxins, perhaps reflecting their biogeographic origins (which include extensive sympatry with bufonids); the tolerance of rodents to bufotoxins also may be related to their physiological resistance to ouabain, a plant cardiac cardenolide (Price and Lingrel 1988; Jaisser et al. 1992). Despite this, surveys have revealed population decline of some rodent species in Australia, and have suggested that poisoning by cane toads may be a potential cause for such declines (Woinarski et al. 2010).

Anecdotal reports suggest that introduced rats (*Rattus rattus*) and native rats (*Hydromys chrysogaster*) kill and consume cane toads. Both species have been observed to either consume body parts of toads, or have dead toads present in their nests (Cassels 1966; St. Cloud 1966; Adams 1967; Covacevich and Archer 1975; Fitzgerald 1990). Does this behaviour occur in other rodent taxa, and if so, do rodents only consume toads in the absence of alternative prey? Taste aversion learning is also important, because predators of many species initially attack and consume toads, but soon cease to do so because of conditioned taste aversion (Webb et al. 2008, 2011). If rodents show this pattern also, then rodent predation on cane toads will occur only in naive predators (e.g. in young animals, or in rodent populations as they first encounter invasive toads). To clarify these issues, we reviewed published literature, conducted field observations and ran experimental trials with three species of native rodents that commonly co-occur with cane toads: the dusky rat (*Rattus colletti*), the pale field rat (*R. tunneyi*) and the grassland melomys (*Melomys burtoni*).

Materials and methods

Field observations

We searched published literature for reports of rodent predation on cane toads, and also assembled observations from our own fieldwork and that of colleagues and others.

Experimental studies

Study area

The Adelaide River floodplain lies 60 km east of the city of Darwin, in the Northern Territory. Maximum monthly temperatures remain above 30 °C year-round, whereas minimum (overnight) air temperatures are lower mid-year. More than 75 % of the annual rainfall comes in less than 4 months, peaking in the period from January to March. However, rainfall shows stochastic variation over many time-scales (Shine and Brown 2008).

Study species

The cane toad (*R. marina*) is native to a wide area of the Americas and was introduced to north-eastern Australia in 1935 as a biological control agent of insect pests of sugar cane (Zug and Zug 1979; Lever 2001). The species has spread through much of tropical and subtropical Australia, and now occurs in Western Australia, a large area of the Northern Territory, most of Queensland and in northern New South Wales (Kearney et al. 2008). In the Australian tropics, metamorphic toads are active by day around the edges of breeding ponds during the dry season, but are dispersed through the landscape during the wet season (Freeland and Kerin 1991; Child et al. 2008a, b). Larger juvenile and adult toads are active at night (Freeland and Kerin 1991) and inhabit a wide variety of habitats, especially anthropogenically disturbed areas (Zug and Zug 1979; Seabrook and Dettmann 1996). Post-larval cane toads span an enormous range of body sizes, from 7 mm (<0.1 g) in recently metamorphosed individuals (Child et al. 2008a) to 180 mm (up to 600 g) in adults (Zug and Zug 1979).

The dusky rat (*Rattus colletti*) is a nocturnal rodent confined to the Northern Territory. Adults range from 60 to 215 g in body mass and their diet includes seeds, rhizomes, corms, grass, fungus and insects (Watts 1977; Williams 1995; Madsen et al. 2006; Menkhorst and Knight 2011). On monsoonal floodplains, these rats can be extraordinarily abundant, reaching 120–635 rats per hectare and biomass up to 4.7 tons km⁻² (Redhead 1979; Madsen et al. 2006).

The pale field rat (*Rattus tunneyi*) is a nocturnal medium-sized rodent (adults 50–210 g) that occurs over much of Australia (Menkhorst and Knight 2011). This species favours dense vegetation along creeks or rocky slopes, and was once common in northern Australia (Braithwaite and Griffiths 1996). Currently, it is patchily distributed in this area (D. Pearson and J. Webb personal observations). It has declined in recent years, and poisoning by cane toads has been implicated as one possible factor in its decline in the Northern Territory (Woinarski et al. 2010).

The grassland melomys (*M. burtoni*) is a smaller (adult size 30–120 g; Menkhorst and Knight 2011) nocturnal rodent found in coastal drainage areas of eastern and northern Australia. It feeds on plant stems, grass, seeds, fruits and insects. It inhabits a wide range of habitats and vegetation types (Watts and Aslin 1981; Menkhorst and Woinarski 1992; Kerle 1995; Menkhorst and Knight 2011).

Collection and housing

Individuals of *M. burtoni* ($n = 42$, mean mass \pm SD: 32.2 ± 6.2 g) and *R. colletti* ($n = 43$, 63.9 ± 21.0 g) were collected from the Adelaide River floodplain, Northern Territory ($12^{\circ}33'20''\text{S}$, $131^{\circ}19'56''\text{E}$ and $12^{\circ}38'59''\text{S}$, $131^{\circ}19'47''\text{E}$, respectively) where they co-occur with cane toads. *Rattus tunneyi* ($n = 10$, 91.6 ± 33.7 g) were collected from Mitchell River ($14^{\circ}49'13''\text{S}$, $125^{\circ}43'17''\text{E}$), Western Australia where toads have yet to invade. At each site, we set approximately 50 aluminium Elliott traps ($33 \times 9 \times 9$ cm) in linear transects at 10 m intervals, baited with rolled oats and vanilla essence or peanut butter. Traps were set at dusk and checked within an hour after sunrise. Captured rodents were weighed, placed in individual calico bags, and taken to the field laboratory (at the Tropical Ecology Research Facility, Middle Point, Northern Territory). Individuals of *R. tunneyi* were air-freighted from Mitchell Plateau to the same field laboratory within four days of capture. All rats were housed in white plastic containers ($60 \times 40 \times 40$ cm; with a shelter site, drinking water and bedding: wood shavings) and exposed to a natural light–dark cycle and temperature (13 h light:11 h dark, ambient air temperature 20–30 °C). We fed the rats with commercial rodent pellets ad libitum, and these pellets were replenished every 2 days.

Metamorphic and juvenile cane toads were collected by hand in the field within 20 km of the Tropical Ecology Research Facility, transferred to the field laboratory, and housed in white plastic enclosures that were positioned on a slope (same containers as described above, with water to create a pond at the lower end and prevent toads from dehydrating, plus grass clippings for shelter). The toads were fed insects ad libitum three times a week until they reached a suitable size for experiments (0.2 g for metamorphs; 3.5 g for juveniles). We defined a juvenile toad as an individual larger than 30 mm snout-urostyle length (SUL) following Cohen and Alford (1993) and Alford et al. (1995). Body sizes (mean \pm SD) of the individuals used in experiments were: metamorph toads: 12.81 ± 0.81 mm, 0.250 ± 0.047 g; juvenile toads: 42.42 ± 7.27 mm, 9.74 ± 5.10 g.

Table 1 Details of sample sizes and treatments in each laboratory experiment to investigate encounters between cane toads (*R. marina*) and native Australian rodents (*M. burtoni*, *R. colletti* and *R. tunneyi*)

Rodent species	Experiment 1. Rodent feeding responses to cane toads	Experiment 2. Evidence of taste aversion (repeated exposure to cane toads: 3 nights)	Experiment 3A. Consumption of alternative food	Experiment 3B. Consumption of cane toads in presence of alternative food
None (control treatment)	1 metamorph toad ($n = 4$)	3 metamorph toads per night (metamorph toad control) ($n = 5$)	Mixed food (food control) ($n = 9$)	Mixed food plus 3 metamorph toads (control) ($n = 8$)
None (control treatment)	1 juvenile toad ($n = 4$)	1 juvenile toad per night (juvenile toad control) ($n = 3$)	3 crickets (control crickets) ($n = 3$)	3 crickets and 3 metamorph toads (control) ($n = 5$)
1 <i>Melomys burtoni</i>	Without a toad present (<i>M. burtoni</i> control) ($n = 4$)	Plus 3 metamorph toads per night ($n = 4$)	Plus mixed food ($n = 11$)	Plus 3 metamorph toads ($n = 4$) ^a
1 <i>Rattus colletti</i>	Without a toad present (<i>R. colletti</i> control) ($n = 3$)	Plus 3 metamorph toads per night ($n = 6$)	Plus mixed food ($n = 6$)	Plus 3 metamorph toads ($n = 6$) ^a
1 <i>Melomys burtoni</i>	Plus 1 metamorph toad ($n = 5$)	Plus 1 juvenile toad per night ($n = 2$)	Plus 3 crickets ($n = 3$)	Plus mixed food plus 3 metamorph toads ($n = 5$)
1 <i>Rattus colletti</i>	Plus 1 metamorph toad ($n = 4$)	Plus 1 juvenile toad per night ($n = 3$)	Plus 3 crickets ($n = 3$)	Plus mixed food plus 3 metamorph toads ($n = 5$)
1 <i>Melomys burtoni</i>	Plus 1 juvenile toad ($n = 3$)	–	–	Plus 3 crickets and 3 metamorph toads ($n = 5$)
1 <i>Rattus colletti</i>	Plus 1 juvenile toad ($n = 6$)	–	–	Plus 3 crickets and 3 metamorph toads ($n = 7$)
1 <i>Rattus tunneyi</i>	Plus 1 juvenile toad ($n = 4$)	Plus 1 juvenile toad per night ($n = 6$)	–	–

For Experiment 3A, Treatment 1 was the control to measure changes in food mass due to desiccation or hydration

n = number of experimental replicates

^a Data for this treatment were obtained from the first night of exposure to *M. burtoni* and *R. colletti* in Experiment 2

Experimental trials

All trials were conducted in a field laboratory, in plastic enclosures as described above, but without bedding. Each enclosure contained a PVC tube (10 cm length, 6.5 cm diameter) for shelter (large enough to accommodate a rat), plus a small pond of water. Because these rodents are nocturnal, we added potential food items at 1830 hours and finished the feeding trials at 0700 hours the following morning. We conducted brief observations every hour from 1900 hours until midnight. In the morning, we recorded whether toads were alive or dead, and which body parts had been consumed. Each rodent was used in only a single trial or in a series of three trials (i.e. one night or three consecutive nights at the most, depending on the experiment). Although many individuals were controls (not exposed to toads, crickets or other food items), all rodents were retained for 4 days following experiments to ensure that they did not show any overt effects of consuming toad tissue or any natural mortality. We did not perform all trial types with *R. tunneyi* because insufficient numbers were collected in the field. Overall sample sizes were low for ethical reasons; these trials included potentially fatal predator–

prey encounters, so numbers of replicates were restricted to the minimum needed to test whether these rodents are likely to be important predators of toads. In some cases, as a result, those numbers were too low to justify statistical analysis.

Experiment 1: Rodent feeding responses to cane toads

Experiment 1 consisted of nine treatments to test whether the three rodent species consume cane toads, and, if so, whether they survive. In treatments where cane toads and rodents were exposed to each other, we offered a metamorph or a juvenile toad to the rodents (Table 1). We had three to six replicates per treatment, and trials ran for only one night.

Experiment 2: Do rodents show evidence of taste aversion?

To assess whether rodents develop an aversion to feeding on toads, we offered metamorph or juvenile toads to individual rodents for three consecutive nights, using seven treatments (2–6 replicates per treatment, Table 1). Fewer

juvenile (1 per night) than metamorph toads (3 per night) were offered to rats due to the larger size of juvenile toads, and the unlikelihood that an individual rat would eat more than one juvenile toad per night. After every trial, we returned the rat to its original enclosure early the following morning. We kept it there (provided with water, food and refugia as described above) until 1830 hours, when it was re-introduced to the (cleaned) experimental enclosure for the next trial with three new metamorph toads or one new juvenile toad.

Experiment 3: Does the availability of alternative food affect rodent predation on cane toads?

We tested if rats will kill and eat cane toads even in the presence of alternative food. First, we tested food consumption and preference by two species of native rodents (*R. colletti* and *M. burtoni*) in the absence of toads, by offering each rat 3 g grass stems, 3 g sunflower seed kernels, 3 g cherries and 3 g raw fish (simultaneously = 'mixed food treatment' below). The grass stems were collected at one of the collection sites of the rats (Anzac Parade, Middle Point, NT). Each food item was set in a small plastic container (7 cm diameter, 3 cm high), with the four containers randomly placed along the centre of the experimental bin. We also offered adult crickets (mean \pm SD total length: 21.8 ± 1.76 mm, mass: 0.50 ± 0.13 g) to the rats as another food treatment. We had six treatments with variable numbers of replicates per treatment (Experiment 3A; Table 1). We weighed remaining mixed food items the next morning and counted number of crickets partially or totally consumed. We accounted for mass changes in food items due to loss (grass, cherries, fish) or gain (seeds) of water over the course of trials using the control treatments (Table 1). The percentage mass gained or lost per container was considered to calculate food consumption by rodents.

To assess if the presence of alternative food modifies predation rates on cane toads, or rodent uptake of other food types, we offered rats a choice of toads versus mixed food (described above) or live crickets (Experiment 3B, Table 1). Every trial ran for only one night.

We recorded the first 3–4 h of 15 trials (Experiment 2 with metamorph toads: *M. burtoni* $n = 4$ trials, *R. colletti* $n = 4$ trials; Experiment 2 with juvenile toads: *M. burtoni* $n = 3$ trials, *R. colletti* $n = 1$ trial; Experiment 3B with metamorph toads: *M. burtoni* $n = 2$ trials, *R. colletti* $n = 1$ trial) with a video camera and a red light (red globe 25-W) to document the behaviour of the rats (e.g. whether they attacked toads, time to kill toads, prey manipulation and consumption).

Data analyses

We recorded the condition (alive, dead) of each rodent and toad at the end of each trial, and categorised the consumption of a toad by a rodent as totally consumed, partially consumed or not consumed. For *R. colletti* and *M. burtoni* in Experiment 1 (feeding responses to cane toads), we compared the number of live and dead cane toads in the presence and absence of rats using Fisher Exact tests in R 3.0.3 software (R Core Team 2013). We did not formally analyse data obtained in Experiment 2 (taste aversion) due to obvious patterns in the results, and low numbers of replicates for some trials. For Experiments 3A and 3B (consumption of mixed food and consumption of cane toads in the presence of mixed food or crickets), we used Kruskal–Wallis tests in JMP 5.0.1 software (SAS 2002) to assess preferences by rodents in the mixed food treatment. We used the mass change of food items (proportion consumed) as the response variable, and the type of food offered as the explanatory variable. Whether or not the presence of alternative food modified the predation rates on toads by rats and their consumption behaviour (tested in Experiment 3B) was simply described; we did not apply statistical tests to these data (for the reasons explained above).

Results

Field observations

Combining published records with field observations, it is clear that two rodent species, the water rat (*Hydromys chrysogaster*) and the black rat (*Rattus rattus*) eat cane toads. Both species have been observed to consume toad tissue, or have dead toads present in their nest sites in the Northern Territory, in Queensland and/or New South Wales. *Hydromys chrysogaster* has been observed directly attacking an adult toad (Electronic Supplementary Material 1). Predation occurs in both urban and rural areas. In some instances where partially consumed toad carcasses have been found in the field, but the predator has not been directly observed, injuries on these carcasses implicate rodent predation. The most likely alternate predators are birds (especially raptors and egrets) that either eat small toads whole (McKilligan 1984) or selectively remove only the tongue of large toads and associated musculature (Beckmann and Shine 2011), resulting in injuries that are inconsistent with those described here. Most other native species do not eat toads (Shine 2010). Cases where other body parts of toads such as internal organs are consumed (a common observation in our study site: G. P. Brown personal communications) are consistent with predation or

scavenging by rodents (Electronic Supplementary Material 1). Importantly, predators did not consume parotoid glands of any dead adult toads found in the field.

Experimental studies

General observations

In the control treatments, all rodents, toads and crickets survived. Rats that were offered cane toads either attacked and killed the toads within a few seconds after the start of trials, or ignored them throughout the trials. Rats often responded to movement by toads, seizing metamorphs with the mouth and seizing juveniles with both the mouth and the paws. The toads were killed by bites to the head or body, and then consumed either partially (including parotoid glands in many instances) or totally. Consumption usually occurred within a few minutes of the attack, but sometimes was postponed for hours. Some rats took toad carcasses back to the shelter site to consume them. Metamorph and juvenile toads that survived exposure to rats were uninjured, and analysis of videotapes showed no evidence of attacks on these individuals.

Experiment 1: Rodent feeding responses to cane toads

Both metamorph and juvenile toads were killed and consumed by *M. burtoni* and *R. colletti*. Although *R. tunneyi* were not tested with metamorph toads, they did kill and consume juvenile toads (Electronic Supplementary Material 2). Mortality rates of metamorph toads were significantly increased by exposure to *M. burtoni* (Fisher Exact $P = 0.048$) and *R. colletti* (Fisher Exact $P = 0.029$). In addition to killing metamorph toads, some *M. burtoni* and *R. colletti* also killed juvenile toads. However, the mortality of juvenile toads in the presence of these predators was not statistically different from mortality in the control treatment (*M. burtoni*, Fisher Exact $P = 0.429$; *R. colletti*, $P = 0.476$).

In all four cases where a *M. burtoni* killed a metamorph toad, it consumed the entire toad. In the case of *R. colletti*, three of the metamorphs killed were totally consumed and one was partially consumed. The only juvenile toad killed by *M. burtoni* was partially consumed, whereas one of the two juvenile toads killed by *R. colletti* was fully consumed and the other was partially eaten. All four *R. tunneyi* killed the offered juvenile toads; two toads were uneaten, and two were partially consumed. All rats survived the trials, and displayed no overt symptoms of toad poisoning. We did not observe symptoms of poisoning such as panting, contractions or convulsion in the rats, as reported for the marsupial *Dasyurus geoffroyi* (Covacevich and Archer 1975) or unsteady gait, loss of righting ability, incapacitation or

tremors, as observed in *Planigale maculata* and *Sminthopsis virginiae* after consuming metamorph toads (Webb et al. 2008, 2011).

Experiment 2: Do rodents show evidence of taste aversion?

Toads exposed to rats suffered high levels of mortality during the three consecutive nights of the trials. Mortality of metamorphs exposed to *M. burtoni* and *R. colletti* was higher than in the control treatment. Both rat species killed similar numbers of metamorphs on each of the three nights (2 or 3 of the 3 toads offered to them were killed each night: *M. burtoni* $n = 12/12$ encounters; *R. colletti* $n = 17/18$ encounters; Fig. 1) with only one *R. colletti* as the exception (3, 3, 1 metamorphs killed on the consecutive nights). Similarly, of the metamorphs that were killed, the number of individuals that were fully consumed did not decline over the three nights. All *M. burtoni* and *R. colletti* completely consumed as many, or more, metamorph toads on night 3 as on night 1 (Fig. 2). As before, all rats survived the three nights of trials, with no overt symptoms of poisoning.

In the same way, the data for predation on juvenile toads show no evidence of taste aversion learning. One of the two *M. burtoni* exposed to juvenile cane toads over three nights did not attack any toads, whereas the other killed and partially consumed toads on the first two nights but did not attack on the third night. For *R. colletti*, one of the three individuals did not attack any juvenile toads, one killed and totally consumed its toad every night, and the third individual ignored the toad on the first night, but killed and partially consumed the toads that were available during the

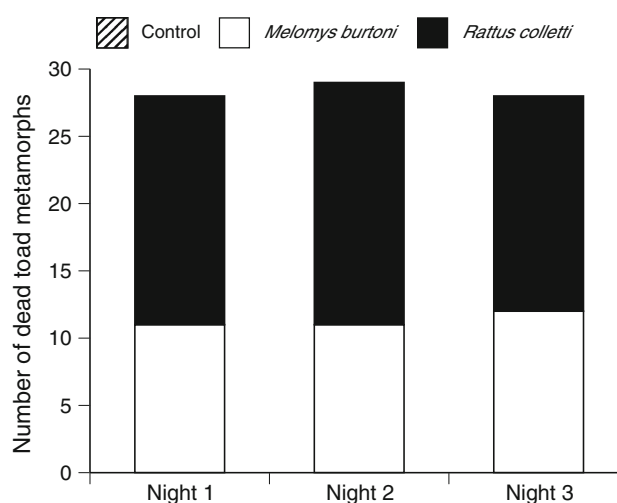


Fig. 1 Number of cane toad metamorphs (*R. marina*) killed when exposed to rodents (*M. burtoni*, $n = 4$ and *R. colletti*, $n = 6$) during three subsequent nights

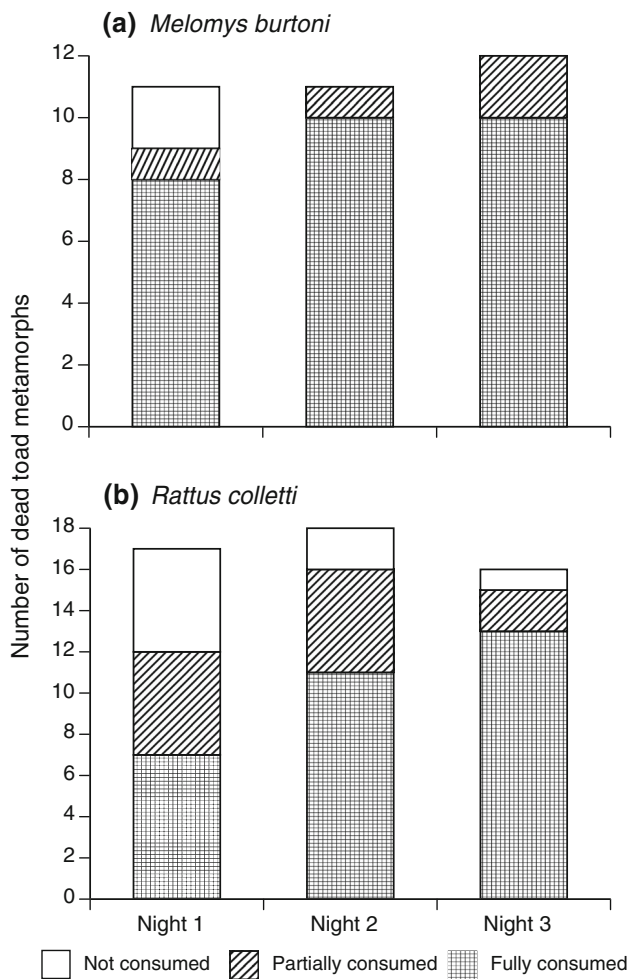


Fig. 2 Number of cane toad metamorphs (*R. marina*) fully consumed, partially consumed, or not consumed by **a** *M. burtoni*, $n = 4$ and **b** *R. colletti*, $n = 6$ in three subsequent nights

second and third nights. Of the six *R. tunneyi*, four ignored toads on each night, one ignored toads on nights 1 and 2 but totally ate the toad on night 3, and one partially ate the toad on night 1 and totally ate the toads on nights 2 and 3. The mass of the juvenile toads totally consumed by the rats (*R. colletti* or *R. tunneyi*) ranged from 6.2 to 13.3 g.

Experiment 3: Does the availability of alternative food affect rodent predation on cane toads?

In the mixed food treatment (Experiment 3A), both *M. burtoni* and *R. colletti* consumed all food types offered. *Melomys burtoni* showed significant preferences (Kruskal–Wallis: $\chi^2 = 35.21$, $df = 3$, $P < 0.0001$), with high mean consumption of cherries and seeds (>50 %) and low mean consumption of grass and fish (<10 %). *R. colletti* did not show clear preferences ($\chi^2 = 1.42$, $df = 3$, $P = 0.700$). *Melomys burtoni* and *R. colletti* readily killed and

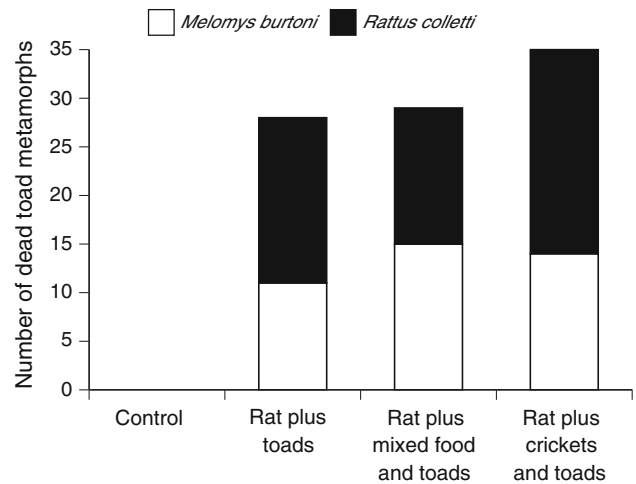


Fig. 3 Number of cane toad metamorphs (*R. marina*) killed when offered to rodents (*M. burtoni*, $n = 10$ and *R. colletti*, $n = 12$) in the absence and presence of alternative food (mixed food or crickets)

consumed crickets when they were the only prey available (all crickets were killed by both species: *M. burtoni*: 7/9 crickets completely consumed, 2/9 partially consumed; *R. colletti* completely consumed all crickets).

Regardless of the presence or absence of alternative palatable food (mixed food or crickets, Experiment 3B), all *M. burtoni* and *R. colletti* killed 2 or 3 of the 3 metamorph toads offered to them in a night, similar to the number of toads killed in absence of other food (Fig. 3). The toads that had been killed were totally or partially consumed, despite the presence of alternative food (Fig. 4a, b). All rats were apparently unaffected by their consumption of toads.

Mixed food was consumed even in the presence of toads, either before or after rodents killed and/or consumed the toads. Food preferences of rodents were unaffected by the presence of toads: preferences by *M. burtoni* differed significantly (Kruskal–Wallis: $\chi^2 = 15.38$, $df = 3$, $P = 0.001$) with high mean consumption of cherries and seeds (>50 %) and low mean consumption of grass and fish (<15 %). *R. colletti* did not show significant food preferences (Kruskal–Wallis: $\chi^2 = 5.026$, $df = 3$, $P = 0.169$). The rate of cricket mortality and consumption was not overtly affected by the presence of toad metamorphs (*M. burtoni*: 10/15 crickets killed, 7/10 completely consumed, 2/10 partially consumed; *R. colletti*: all crickets killed, 17/21 completely consumed, 3/21 partially consumed).

Discussion

Recent studies in Australia have suggested that poisoning by cane toads may threaten some types of mammals

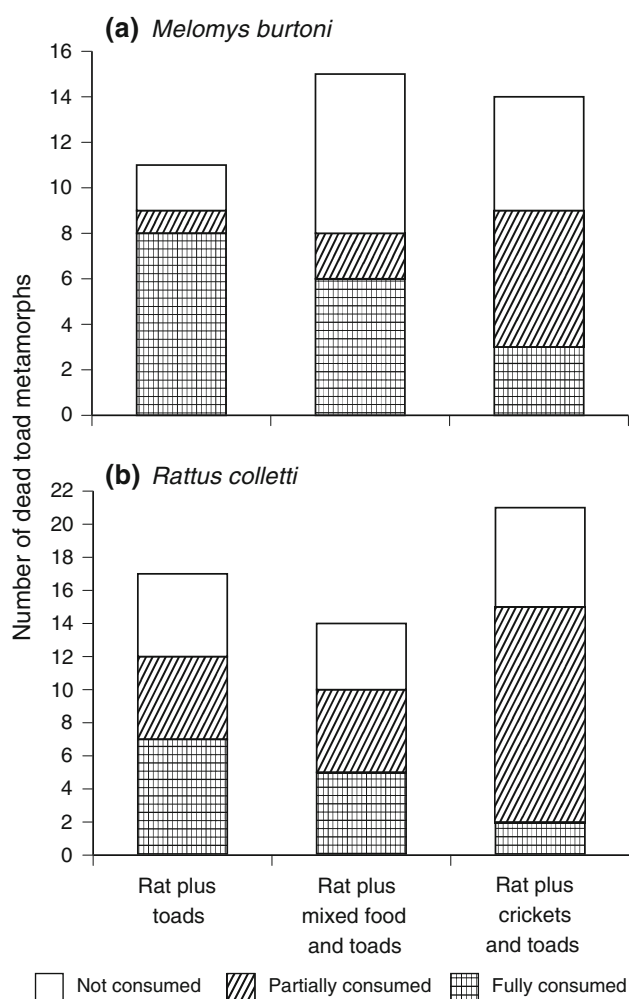


Fig. 4 Number of cane toad metamorphs (*R. marina*) fully consumed, partially consumed and not consumed in the absence and presence of alternative food (mixed food or crickets) by **a** *M. burtoni*, $n = 10$ and **b** *R. colletti*, $n = 12$

including rodents (Woinarski et al. 2010). In contrast, our data indicate that rather than threatening rodent populations, invasive cane toads represent an additional food source for these animals. Our laboratory results demonstrate that three species of native rodents (a) readily kill and eat toads; (b) do not suffer overt ill effects from consuming toad tissue; and (c) continue to eat toads after their initial exposure, rather than excluding toads from the diet due to conditioned taste aversion. Published information, our observations in the field, and our results from experimental feeding trials, all show that Australian rodents can prey upon live cane toads (and likely, also scavenge upon their bodies) with no apparent ill effects on the rat's health or behaviour. Many rodents are opportunistic omnivores (Watts and Aslin 1981; Breed and Ford 2007) and both captive and wild rats have been observed attacking and consuming anurans (Bernard 1974; Watts and Aslin 1981;

Posner and Miley 1982; Thurley and Bell 1994; Olsen 1995; Smales and Cribb 1997).

Extrapolating the results of our experiments to the wild (i.e. to the occurrence of predation on cane toads by rats in nature) is difficult. However, anecdotal observations confirm instances of predation on toads by both native rats (*H. chrysogaster*) and introduced rats (*R. rattus*; Cassels 1966; St. Cloud 1966; Adams 1967; Fitzgerald 1990). The frequent discovery of partly consumed bodies of toads, and high predation rates on radio-tracked toads in dense vegetation where birds would be unable to attack them (G. P. Brown, personal communications—Electronic Supplementary Material 1) further support the inference that rodents are important predators on invasive toads in tropical Australia.

Although rodents are capable of taste aversion learning (Rozin and Kalat 1971), they are physiologically capable of dealing with many toxins present in tissues of both plants and animals (e.g. alkaloids, cardiac glycosides, glucosinolates, tannins—Ruiz et al. 1977; Glendinning 1990; Xiao et al. 2008; Samuni-Blank et al. 2013). Predators are unlikely to develop taste aversion to a given prey type if they cannot detect it by taste, if they obtain nutritional benefit from it, or if they are not imperilled by the toxins that it contains. This appears to be the case with cane toad tissues. In our experiments, *M. burtoni*, *R. colletti* and *R. tunneyi* continued to consume metamorphosed or juvenile toads over three consecutive nights. It remains possible that aversion might develop over a longer term, but the effects of bufadienolide poisoning have very rapid onset (within 10–25 min after toad consumption; Webb et al. 2008, 2011). It is more likely that rodents tolerate toad toxins, as our experimental individuals did not show any effects of poisoning over 4 days. In the wild, rats are exposed to a wide array of potential food types, so that consumption of a given food in the laboratory may not translate into consumption of that food in the field (because more palatable items are on offer). However, in the present work *R. colletti* and *M. burtoni* showed no reduction in their rates of toad consumption even when alternative food was provided (Experiment 3B).

Rodents can locate motionless food by scent and taste (Whishaw et al. 1998), but our observations suggest that attacks by all three rodent species occurred in response to movements by prey (toads or crickets). *Rattus colletti* and *M. burtoni* consumed small (metamorph) toads at higher rates than larger (juvenile) toads. That difference may reflect ontogenetic changes in toxin contents of the cane toads (metamorphs contain less toxin than juveniles: Hayes et al. 2009). The keelback snake *Tropidonophis mairii* is resistant to toad toxins, but selectively consumes ontogenetic stages of the toad that contain less toxin (Llewelyn et al. 2012). Rat responses may be affected not only by

toxin content but also by prey size per se; some of the smaller rats fled from larger juvenile toads rather than attacking them. Although our sample sizes are small, the *R. colletti* and *R. tunneyi* that attacked and killed large (juvenile) toads on all three nights of their trials were the largest individuals that we tested (117.5 and 158 g, respectively). Thus, prey size relative to predator size may influence propensity to attack and or consume (e.g. Paine 1976). As a result, even large adult cane toads may be at risk from large rat species such as *Hydromys chrysogaster* (up to 1,200 g) and *Rattus rattus* (up to 300 g). Interestingly, field observations on large toads attacked by rats and toad carcasses found in rat burrows or on the edge of waterbodies, suggest selective feeding on soft toad body parts that are low in toxin content, but some rats eat most of the toads' skin, organs and muscle (see Electronic Supplementary Material 1). Although predation is difficult to observe in the field, the food-hoarding behaviour of some rodents (Watts and Aslin 1981) might provide an opportunity for more extensive studies on predation of cane toads by other species of rodents in Australia.

At an ecological level, how significant is rodent predation on cane toads? That is, do cane toads increase food availability for rodents, and does predation by rodents substantially reduce cane toad abundance? We can only speculate as to the answers to those questions. Toad arrival will have both direct and indirect effects on food availability for rats. In terms of direct effects (rats eating toads), the biomass of these slow-moving easily-captured prey can be very high (Ward-Fear et al. 2009), especially in the years immediately following toad arrival at a site (Freeland 1986). Indirect effects may well be even greater. Fatal toxic ingestion of toads virtually eliminates populations of previously-common predators such as large varanid lizards and quolls (Ujvari and Madsen 2009; Woinarski et al. 2010), thereby reducing predation on rats, as well as enhancing the abundance of taxa that were the prey of those impacted predators (Doody et al. 2006; Shine 2010; Brown et al. 2013). Other interactions such as competition for food between native rodents and adult toads are unlikely to be important. Insects (mainly grasshoppers) comprise a small proportion of the rodents' diet (Watts 1977; Kerle 1995; Menkhorst and Knight 2011), whereas adult toads prey mostly on insects, occasionally on other arthropods and rarely on vertebrates (Zug and Zug 1979; Freeland et al. 1986). In combination, then, toad invasion could conceivably increase rat numbers and stated concerns about declines of rodents in Australia due to toad invasion (e.g. Woinarski et al. 2010) can be reviewed in light of our findings.

Whether or not predation by rats affects toad population densities is a more difficult question. Despite the high fecundity of cane toads, their populations in Australia may be

sensitive to changes in juvenile and adult mortality (Lampo and de Leo 1998); hence, rodent predation could potentially reduce toad densities in areas where rats are abundant. However, large year-to-year fluctuations in abundance of both toads and rats, driven by abiotic factors (especially, rainfall: Redhead 1979; Alford et al. 1995; Madsen and Shine 1999) may obscure (and perhaps, weaken) any influence of predators on toad demography, as well as effects of the availability of toads on rat abundance and demography. Nonetheless, one clear result from recent research is that cane toads in Australia are vulnerable to predation by a wider range of native species than was previously assumed to be the case (Ward-Fear et al. 2010; Beckmann and Shine 2011; Cabrera-Guzmán et al. 2012). The present study adds rodents to that list of toad predators. Biotic resistance to the Australian invasion, thus may be an important constraint on cane toad success; some native predators can potentially reduce the numbers of individuals of this species and may help to explain the often-reported decline in toad abundance post-colonisation (Freeland 1986).

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